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PRESERVED VISUAL IMAGERY IN VISUAL FORM AGNOSIA

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Abstract—We investigated the ability of a patient (D.F.) with profound visual form agnosia to perform a variety of tasks requiring visual imagery. Despite her inability to discriminate between objects and patterns of different shapes, sizes, and orientations, D.F. showed quite normal visual imagery involving these same 'visual' properties when the images were drawn from long-term memory. Thus, she was able both to scan mental images in search of particular features and to form new images by combining several known images. While there is growing evidence that perception and imagery share common neural substrates, the fact that D.F. shows intact visual imagery in the face of a massive perceptual deficit in form vision challenges recent suggestions that these two psychological processes share common input pathways in early vision. It is suggested that regions in the occipitotemporal pathway may be important for the generation of visual images while regions in the posterior parietal system might be involved in the manipulation of these images.

Key Words: visual agnosia; visual imagery; object recognition; cortical visual pathways.

INTRODUCTION

Although there have been a few informal observations of the apparent preservation of visual imagery in patients with visual agnosia, until recently no systematic assessments of this phenomenon have been made (for review, see [17]). Some early work suggested that patients with visual form agnosia [4] could retrieve, to some degree, the shape of common objects from memory, but few details were provided [1, 5, 13]. In addition, a patient described by Adler [1] was able to make some crude but recognizable drawings of common objects from memory. More systematic investigations of imagery in such patients are potentially quite important, however, in view of the recent claims by Kosslyn that visual imagery not only depends on the same neural substrates as visual perception but a critical component of image generation is the activation of circuitry very early in the cortical visual pathways that mediate perception [43].

Recent work by Behrmann *et al.* [3] with a patient showing visual agnosia of the associative type [17] provides convincing evidence that it is possible to retain well-preserved visual imagery despite having a profound deficit in object identification. Although their patient (C.K.) could describe the form of objects from memory and could produce highly accurate copies of objects, he had great difficulty identifying line drawings

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of common objects and could not recognize letters of the alphabet. Nevertheless, despite these perceptual difficulties, C.K. showed excellent visual imagery. A patient with a similar dissociation between perceptual report and visual imagery has been described by Jankowiak *et al.* [37]. This patient (M.D.) had bilateral lesions in the occipitotemporal area that left him with a severe deficit in object identification. But again, M.D., like C.K., seemed to have relatively intact visual imagery.

These two studies would appear, at first blush, to challenge Kosslyn's [43] claim that visual imagery depends on the activation of primary visual cortex and other early visual processing areas. After all, if, as Kosslyn argues, output from these early visual areas is "processed in the usual ways—regardless of whether the activity arose from immediate input from the eyes or from information stored in memory" (p. 336 [43])—then these patients, who appear unable to process perceptual input in a normal fashion, should also show a deficit in visual imagery. But then, C.K. and M.D.'s abilities to deal with "bottom–up" inputs, while impaired, are not completely compromised. M.D., for example, could still identify 50% of the black-and-white drawings he was shown and could always make correct same–different judgements when presented with two drawings at the same time. C.K. could identify faces and could also copy line drawings he could not identify. Perhaps the difficulty in these two patients was one of grouping/segmentation (as Moscovitch *et al.* have suggested in a recent paper [58]) and they might still have been able to deal with input from early visual areas when that input arose from top–down activation from stored representations of objects. What is needed to challenge Kosslyn's proposal more directly is an evaluation of the imagery in a patient whose inputs from early visual areas to downstream object identification networks are so thoroughly damaged that the patient cannot perceive the form of even the simplest of visual stimuli. To this end, we report here the results of an imagery study in the patient D.F. who has a profound visual form agnosia and whose perceptual abilities are much more compromised than those of either C.K. or M.D. As will become evident, despite her severe perceptual deficits, D.F. shows excellent visual imagery.

Patient D.F., whose brain damage was caused by anoxia, shows the classic signs of visual form agnosia—not only does she have great difficulty recognizing common objects and familiar faces but she is also unable to discriminate even simple geometric forms. In one study [35], for example, D.F. was able to identify only 11% of 120 line drawings of common objects that were presented to her (although she could identify nearly 75% of the real objects on the basis of their colour and visual texture). At some level, however, she can still process form information, given that she has preserved object-directed reaching and grasping movements [26, 27, 29]. Thus, when she was asked to pick up various objects placed one by one in front of her, the calibration of her grasp during the execution of the movement reflected the size, shape, and orientation of the target object, even though she was unable to perform a simple perceptual matching task with the same stimuli or discriminate between them [28, 29]. For example, when she was asked to pick up each of a series of equal-area blocks that varied in their surface dimensions, the opening of her hand accurately reflected the width of the target block—and this was achieved well before contact with the block. Yet when presented with pairs of these blocks in a same–different judgement task, her performance was at chance. Similarly, she could not indicate the width of a block by opening her index finger and thumb. Taken together, these results suggest that while D.F.'s visuomotor systems still have access to information about the size, shape, and orientation of objects, she can no longer use form information to 'perceive' the identity of objects or discriminate between them.

But how does D.F. do on imagery tasks where she has to access long-term visual representations of object form? Some earlier work work by Servos *et al.* [71] showed that D.F. was able to make drawings of common objects from memory—a behaviour that might require the long-term representation of form (see [76]). They found that when D.F. was asked to draw a series of 22 common objects from memory (objects she would have encountered before the anoxic event), she produced quite recognizable drawings even though she was unable to identify good line drawings of these same objects on a later occasion. In another task, she was able to indicate the width of an imagined object with her finger and thumb (e.g. "Show me how wide a 4 inch block would be") [29]. Finally, a recent study by Goodale *et al.* [25] has shown that D.F. can make use of stored visual images from long-term memory to control 'pantomimed' grasping movements (e.g. "Show me how you would pick up a grapefruit" or "Show me how you would pick up a raspberry"). It is also intriguing that D.F. not only has visual dreams but she reports that the objects in her dreams are vivid and well-structured [L. S. Jakobson, personal communication].

Although these studies provide some indication that D.F. still has access to long-term representations of object form, it was possible that in some cases she was simply using propositional information about certain object features such as relative size, rather than a mental image of the object, to generate the correct response. In addition, in many cases, the evidence for imagery was derived from motor responses such as drawing or pantomime, where motor routines rather than actual images might have been used. Moreover, we had no information about whether or not she could manipulate the visual images in any way. Thus, the main purpose of the present study was to carry out a more rigorous investigation of D.F.'s ability to generate visual images. We reasoned that if she was truly capable of generating visual images than she should be able to manipulate these images in cognitive tasks in which she was required either to scan images in search of particular features or to form new images by combining several known images. Finally, on the basis of the pattern of damage in D.F.'s brain, some inferences were made about which brain regions might be critical for visual imagery.

METHOD

The patient

At age 34, the patient D.F. suffered irreversible brain damage as a consequence of carbon monoxide poisoning. She was 37 when the present testing was carried out. Magnetic resonance imaging carried out approximately 1 year after the anoxic event revealed a pattern of diffuse brain damage consistent with anoxia—although damage in the cerebral cortex appeared to be largely restricted to the ventral portion of the lateral occipital region, primarily in areas 18 and 19 (bilateral) but with apparent sparing of areas 17, 20, 21 and 37 (further details can be found in Ref. [53]). Neuropsychological and psychophysical testing revealed the presence of a profound visual form agnosia. Not only could D.F. not identify line drawings of common objects, but she also failed to discriminate between horizontal and vertical gratings, or between simple geometric shapes such as a triangle and a square. This failure to identify or discriminate between different forms was observed regardless of which stimulus parameters were used to define the contours—intensity, colour, texture, stereopsis, motion, proximity, continuity, or similarity. Her perceptual reports of colour were essentially normal and she could use this cue, together with other surface features such as visual texture, to identify real objects or even colour slides of objects, much better than she could line drawings. Psychophysical testing revealed that her visual form agnosia could not be reduced to a simple sensory deficit. D.F. is right-handed and her Wechsler–Bellevue verbal IQ was found to be in the normal range [52, 53]. A control subject, who matched D.F. with respect to sex, age and handedness, was also tested.

Visual imagery tasks

We used a series of imagery tasks that have appeared in the literature. All of them involved in some way the scanning of visual images and the assessment of their structure. Four classes of task were used: size and dimension discriminations, scanning for particular features, motor imagery, and image construction.

Size discriminations. Prior work suggested that subjects tend to use visual imagery when required to make size discriminations between common objects (e.g. "Which is bigger, a camel or a cat?") and that subjects are more likely to make use of visual imagery when the size discriminations are difficult (e.g. "Which is bigger, a camel or a horse?") [46, 47, 60]. We generated a series of 60 pairs of items based on the norms produced by Paivio [60]. Thirty of the pairs involved animals and the remaining 30 pairs involved non-living objects. Each of the 30 pairs was further divided into groups of 15 pairs which contained either easy discriminations (mean differences of at least 2.0) or difficult ones (mean differences of less than 0.5). Further details of the ranking system can be found in Paivio [60]. A second imagery task involving size required judgements about whether or not a particular object was taller than it was wide. The 24 items were taken from those used by Kosslyn *et al.* [45]. Twelve of the items were taller than they were wide whereas the remaining items were wider than they were tall.

Feature search. These tasks involved generating a visual image of a letter or an object and then scanning it in order to identify particular features.

One task, adapted from Kosslyn *et al.* [45], involved deciding whether or not the ears of a particular animal protruded above the skull or flopped along the side of its skull. Presumably, this sort of task requires visual imagery [39, 46].

Another series of scanning tasks involved the letters of the alphabet. One task required D.F. to name all of the upper-case letters which were composed of only straight lines. Another task required her to name all of the upper-case letters which had some curves in them. Yet another task required her to list all of the lower-case letters composed only of straight lines. Finally, a task was used which required D.F. to list all upper-case letters which contained a vertical line at the far left of the letter. These letter tasks are based on tasks described by Kosslyn *et al.* [45]. Previous work suggests that visual imagery is needed to perform such tasks [45].

Motor imagery. Given that D.F.'s motor behaviour is intact—not only gross movements such as walking but also skilled movements such as visually guided reaching—we were interested in seeing whether or not her memory for movements was also preserved. Although it is not clear at this point what sorts of processes underlie memory for movements (i.e., motor codes, spatial codes, elements of form processing, or some combination of all of these), it is likely that visual imagery plays some part in it [14, 38, 68, 72]. To assess motor imagery in D.F., we used the list of 50 true-or-false items developed by Goldenberg *et al.* [23]. A typical question might be: "Can one touch the left heel with the left hand without bending the knee?"

Image construction. Not only can visual imagery be used to scrutinize previously encoded images for particular features, it can also be used to combine two or more images to generate emergent features and forms which can be identified (see [19, 20]). We investigated D.F.'s ability to construct visual images, using some of the items constructed by Finke *et al.* [19]. For example, one item went as follows: "Imagine the letter 'D', rotate it 90 degrees to the left. Put a triangle directly below it having the same width and pointing down. Remove the horizontal line. Now describe what the object resembles most." The correct answer in this case would be "ice-cream cone." Finke *et al.* [19] initially presented their subjects with visual exemplars of the items they were to image and took them through some examples of how the various figures could be combined to generate new patterns. Given D.F.'s perceptual deficits, we were unable to use these exemplars, and we therefore presented her with only a subset (6) of some of the less complicated items used by Finke *et al.* [19].

Letter identification

In order to compare D.F.'s visual imagery of letters with her attempts to perceive them, we presented her with a series of 52 large high-contrast laser-printed letters ('a–z' upper and lower case) one at a time. The letters measured approximately 6 mm × 6 mm and were presented in front of D.F. at arm's length (approximately 40 cm away).

Procedure

Testing was conducted in a room in which there were no pictures or printed materials visible. In all of the imagery tasks reported, D.F. and the control subject were not allowed to trace out shapes on the table or in the air. No time restrictions were given and D.F. did not require more time than the control subject to complete the visual imagery tasks. Testing took about 3 hr to complete and was carried out over two sessions. The letter imagery tasks and the letter identification task were not administered during the same session.

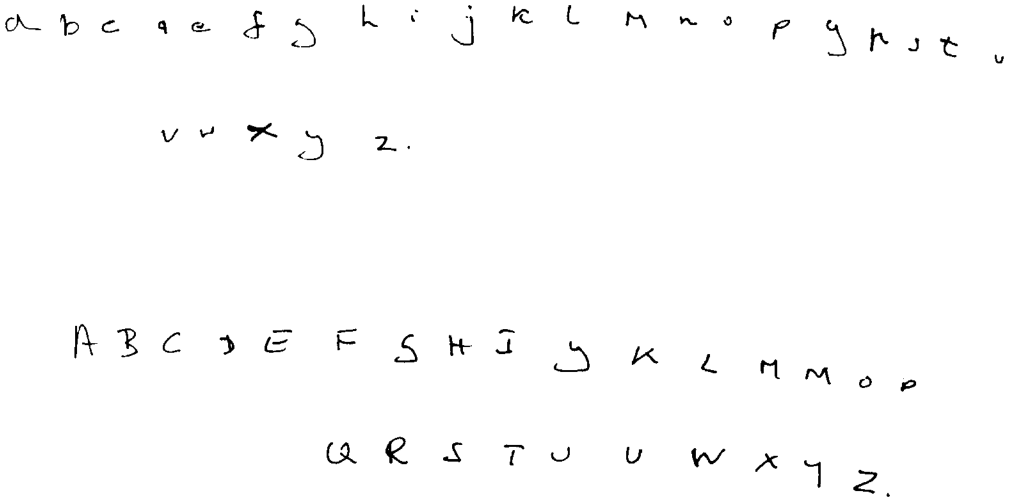

Fig. 1. D.F.'s drawings from memory of lower- and upper-case letters of the alphabet.

Table 1. Number of correct answers for patient D.F. and the control subject on various visual imagery tasks. Numbers in brackets represent the maximum score. See text for descriptions of tasks

Task	D.F.	Control
Size (60)	59	60
Taller–wider (24)	23	24
Animal ears (20)	18	17
Curves (11)	11	11
Left vertical (12)	11	12
Upper–lower-case (24)	23	24
Motor imagery (50)	45	45
Image construction (6)	3	4

Results

D.F. had great difficulty in the letter identification task, managing to name only 8 of the 52 letters presented to her. This is in marked contrast to her preserved ability to draw the letters of the alphabet from memory (see Fig. 1). Moreover, as Table 1 shows, D.F.'s performance in the visual imagery tasks involving letters was indistinguishable from that of the control subject. The only mistakes she made involved the upper-case letter 'N'. One can see in Fig. 1 that she also had some trouble drawing the letter 'N'—making it resemble the letter 'M'.

As Table 1 makes clear, D.F.'s performance in all of the other visual imagery tasks was virtually identical to that of the control subject and in most tasks, except 'image construction' they both achieved near-perfect scores. Not only has she retained the ability to compare images on the basis of size and to scan them for particular features, but she can combine two images and identify the emergent pattern that results.

DISCUSSION

The present results provide clear evidence that D.F. has access to long-term representations of object form despite being unable to use form information for visual object recognition. Her performance on all of the visual imagery tasks was comparable to that of the control subject and to that of other normal subjects tested on similar tasks in the literature. Not only could D.F. successfully scan visual images for particular features, but she could also construct and identify new visual images by combining two or more images. D.F.'s preserved visual imagery may also have contributed to her ability to draw pictures of common objects from memory in an earlier study [71]. In all of these instances, then, D.F. appears to have access to form information even though her perception of form is severely impaired. In the present study, for example, she was able to identify only 8 of the 52 letters presented to her even though she clearly had no difficulty in scanning the visual features of letters from memory and was able to print out all of the letters of the alphabet.

It might be tempting to conclude from this that there are separate neural systems for object perception and visual imagery. A more parsimonious interpretation, however, is that both visual object perception and visual imagery are subserved by a common visual representational system [3, 15–17, 42, 43, 74], but that, in D.F.'s case, the critical sensory input to this common system is defective or absent, whereas the access route from stored memories of objects is still intact. What is not supported by the findings in D.F., however, is the recent proposal by Kosslyn [43] that a critical component of the circuitry that imagery shares with perception is the set of cortico-cortical projections from primary visual cortex to higher-level visual processing areas.

Kosslyn proposes that when we engage in imagery, we make use of the explicit retinotopography of V1 and other low-level visual areas in the occipital lobe by activating these regions via the same back projections from visual memory that are used in top–down hypothesis testing during normal perception. The normal downstream projections from V1 to higher visual areas are then activated (just as they would be in normal perception) and it is this downstream activation that leads to the imagery experience. In support of this claim, he and others have used PET and functional magnetic resonance imaging (fMRI) to show activation in the region of primary visual cortex while subjects are performing imagery tasks [44, 48]. Although other workers [66, 67] have not found such activation, there is some dispute over whether or not the appropriate baseline conditions were used in these studies [48]. But even if V1 and other low-level visual modules are often activated during imagery, this does not mean that this activation is necessary for imagery to occur. Such activation may be merely an occasional epiphenomenon associated with the activation of higher-level visual processing modules by back-projections from stored visual memories. The critical tests of Kosslyn's ideas must come from neuropsychological studies which examine imagery in individuals who have sustained damage either to V1 or to output systems from V1 to higher-level modules downstream.

The neuropsychological evidence on this point is sparse and contradictory (for review, see [21]). Farah and her colleagues, for example, have reported that unilateral occipital lobectomy restricts the 'size' of visual images that the patient can generate [18]. In contrast, Goldenberg and his colleagues describe a patient who appears to have vivid imagery despite having dense cortical blindness following almost complete destruction of primary visual cortex [22]. It is possible, as Goldenberg and his colleagues suggest, that spared islands of primary cortex in this patient might have mediated the preserved visual imagery that they observed. It is also possible that their patient had normal imagery that was not dependent on these spared regions of primary visual cortex, and that the apparent 'shrinkage' in the maximum size of visual images in the patient studied by Farah *et al.* [18] was due, not to damage to primary visual cortex *per se*, but to some sort of depression of downstream visual areas that normally mediate imagery.

While the evidence from lesions of primary visual cortex is somewhat equivocal, the present study, in which the patient D.F. shows apparently normal imagery in the face of a massive perceptual deficit, suggests that whatever mechanisms are mediating imagery they do not require inputs from primary visual cortex that normally carry perceptual information. If they did, then D.F., who cannot use bottom–up visual information about visual form to mediate even the simplest of same–different judgements and matching tasks, should show greatly diminished visual imagery for object form. One should keep in mind, however, that not all visual inputs for the processing of form information are compromised in D.F. Thus, even though she is impaired in the use of form information for perception she can still use form information to modulate her grasping movements directed at objects [26–29]. For example, as mentioned in the Introduction, she is able to pre-shape her hand to anticipate the size, shape and orientation of target objects that she is asked to pick up, even though she is unable to discriminate the same objects in a perceptual task [26–29].

The dissociation between D.F.'s inability to use form information for perception and her ability to use it for the control of skilled grasping movements was an important piece of evidence in a recent theoretical account of the organization of the primate visual system put forward by Goodale and Milner [24, 28, 51]. They proposed that the neural systems processing the visual information used in object recognition are relatively independent of those mediating the visual control of skilled action. They also suggest that this functional distinction between different kinds of visual processing can be mapped onto the two streams of visual processing that have been identified in the primate cerebral cortex—the ventral stream projecting from primary visual cortex to the inferotemporal region and the dorsal stream projecting from primary visual cortex to the posterior parietal region [75]. This distinction is rather different from the "what versus where" dichotomy proposed initially by Ungerleider and Mishkin [75]. In Goodale and Milner's scheme, both streams are seen as using information about objects and their locations; each stream, however, uses this information in different ways. According to Goodale and Milner, transformations carried out in the ventral stream, which focus on the enduring characteristics of objects and their spatial relations, permit the formation of long-term perceptual representations that are used to identify and recognize objects; those carried out in the dorsal stream, which utilize moment-to-moment information about objects and their location in egocentric frames of reference, mediate the visual control of skilled actions, such as manual prehension, that are directed at those objects. In the case of D.F., then, it is possible that there is sparing of the inputs to the dorsal system whereas the inputs to the ventral system, particularly those concerned with object form, appear to be compromised.

Given D.F.'s pattern of brain damage and the functional dissociations that have been observed in her visual abilities, one can use the scheme put forward by Goodale and Milner [24, 28, 51] to speculate about which cortical regions might be mediating her apparently normal visual imagery. D.F.'s brain damage, of course, was caused by anoxia and one must be cautious therefore in drawing strong conclusions about what pathways might be spared and what pathways might be compromised in her brain. Much of the damage that is evident, however, appears to be restricted to areas 18 and 19 in the ventrolateral occipital lobe, leaving area 17 relatively intact as well as much of the temporal lobe (including areas 20, 21 and 37). The ventrolateral region of the occipital lobe may contain regions corresponding to some of the early processing modules of the ventral stream. Thus, if these areas were compromised in D.F., visual information about object form would no longer reach the later processing stages in the ventral stream (although such information can apparently reach regions in her posterior parietal cortex that mediate her intact visuomotor behaviour).

One of the consequences of damage to relatively early regions in the ventral stream, such as areas 18 and 19, might be to produce deficits in the integration processes that underlie visual perception. Moscovitch *et al.* [58] have recently suggested that the grouping/segmentation processes which are critically required during the early stages of bottom–up visual perception are not necessary in the top–down processes that mediate visual imagery. In other words, the very nature of visual imagery is to generate individual components of an object which automatically results in object segmentation. It might well be that areas 18 and 19 (which appear to be damaged in D.F.) play a critical role in these grouping processes and as a consequence D.F.'s visual perception is compromised even though her visual imagery is not. But whatever visual pathways were damaged in D.F., it is clear that they are not critical for visual imagery and it is equally clear that the striking dissociation between D.F.'s perceptual and imaging abilities is not consistent with Kosslyn's proposal that perception and imagery share common circuitry at relatively low-levels in the cortical visual system.

It seems likely, therefore, that intact structures in D.F.'s ventral stream are mediating her ability to generate images of object form. Consistent with this idea are observations suggesting that regions within the temporal lobe of monkeys and humans mediate both object perception and the long-term representation of form [8–10, 31, 33, 36, 40, 54–56, 62, 69, 70]. Moreover, unlike primary visual cortex for which there is little evidence for intrinsic attentional modulation of activity in either the monkey [11, 57; but see 59] or the human [7, 32, 34, 41, 49], there is a good deal of evidence to suggest that attentional modulation is a common feature of modules in the ventral stream from V4 through to inferotemporal cortex (for review, see [24]). These observations coupled with mounting evidence that object perception and visual imagery share common mechanisms [3, 15–17, 42, 43, 74] suggest that the occipitotemporal system is critical for the generation of images. Indeed, recent studies using functional neuroimaging have directly implicated this region in visual imagery for object form [23, 44, 65, 66].

In contrast to the occipitotemporal system's role in visual image generation, the parietal cortex might play a role in certain image transformations such as mental rotation [12, 16, 61, 64, 65] although the parietal lobes do not appear to be critical for the long-term encoding of object form [10]. In other words, one of the functions of the posterior parietal region might be to act as a sort of buffer for visual transformations although no long-term representations of object form are actually stored there.

As discussed earlier, in addition to the possible role of the parietal lobes in object rotation, there is mounting evidence that this region also processes form information for the control of skilled action such as visually-guided reaching and grasping movements. For example, work in the monkey has demonstrated that some cells in the posterior parietal cortex not only fire when the monkey manipulates an object but are also visually sensitive to the size and orientation of that object [73]. Recent neuropsychological results from a parietal-lesioned patient (with intact temporal lobes) are consistent with this role of the parietal cortex. Goodale and his colleagues describe a patient who can no longer appropriately shape her hand to reflect the shape of objects that she is required to pick up, even though she has no difficulty in discriminating between these same objects in a perceptual task [30].

While the mechanisms mediating the visual control of action and those mediating the manipulation of visual images might both be in the posterior parietal region, they could be located in rather different regions [50]. Specifically, the action systems, which correspond to the ancient dorsal stream of monkeys, appear to be located in the superior regions of the posterior parietal lobe—regions in which damage results in visuomotor deficits [63]. The systems supporting the transformation of mental images, however, may be located in more ventral regions of the posterior parietal cortex, where it has been proposed that input from both the ventral and the dorsal stream send converging projections [50]. The mechanisms in these region that are responsible for mental rotation and other forms of image transformation (such as the 'Image Construction' Task used in the present study) might make use of egocentric frames of reference that are related to those used by the dorsal stream. In other words, one might speculate that some of the high-level cognitive systems that mediate image transformation, particularly with respect to the 'observer's' viewpoint, have evolved from the more ancient visuomotor systems supporting the control of skilled actions.

Whatever the role of the posterior parietal cortex might be in image transformation, it is clear that its role in the control of skilled action requires mechanisms with much shorter temporal constants than those operating in the ventral perceptual system. Indeed, it has been suggested that the control of visually guided reaching and grasping movements demands that the size, shape, and orientation of goal objects be computed *de novo* each time they are encountered, since the position and disposition of an object within egocentric frames of reference (i.e. with respect to the eye, head, body, and/or limbs) can change dramatically from one moment to the next. The ventral stream, however, because it is more concerned with developing long-term representations of objects for indentification and recognition, is not subject to such temporal constraints (for discussion of this issue, see [24, 28, 51]).

One strong piece of evidence for this temporal distinction comes from work with patient D.F. In one study, D.F. was initially presented with a target object which was then removed, and then she was required to pantomime a grasping movement towards it. With delays of as little as 2 sec, her grasping movements became quite unrealistic and did not at all reflect the size and shape of the object [25]. With no delays, of course, her grasps were quite normal. This suggests that the processing of form information in the dorsal stream is relatively short-lived. Remember that in the case of D.F., the direct visual input about form to the common visual imagery/object perception system (presumably corresponding to the ventral stream) is likely absent and, therefore, the form of a newly encountered object cannot be encoded (even though her dorsal stream can use the information to control grasps in real time). D.F. is still able, however, to access long-term information about object form for the control of her reaching and grasping movements. For example, as was mentioned earlier, she can produce pantomimed movements to objects about which she has knowledge (e.g. "Show me how you would pick up a grapefruit") [25]. How such stored information about object size and form reaches the motor system (and interacts with 'on-line' information from the dorsal stream) is not well understood, although there is evidence for anatomical connections between visual areas in the temporal and posterior parietal cortex [2, 6]. But whatever the routes might be from memory to motor act, such pathways seem to be quite intact in D.F. Moreover, as we have seen in the present study, D.F. can use long-term visual representations not only to control her motor acts, but also to perform purely 'cognitive' manipulations of visual images.

In summary, it seems likely that the generation of images for the kinds of cognitive tasks used in the present study depend in D.F. on intact representational mechanisms in the ventral stream of projections to the temporal lobe (and not on activation of mechanisms in primary visual cortex). At the same time, some manipulations of these representations may depend upon 'on-line' mechanisms associated with (or derived from) the dorsal stream of projections to the posterior parietal cortex—mechanisms that use egocentric frames of reference. In some sense then, the functions of the ventral and dorsal streams in the generation of visual images and their manipulation might be seen as paralleling their role in the mediation of perception and action based on direct visual input.

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